

Redistribution of Nutrients in Subtropical Rainforest Trees

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Fresh foliage and leaf litterfall from trees and understorey plants in a N.S.W. subtropical rainforest were chemically analysed to estimate nutrient redistribution. In general, the proportion of nutrients redistributed in these species at time of leaf litterfall is low. Results available on nutrient redistribution from the same species in this area during heartwood formation showed that trees which redistributed phosphorus from foliage, redistributed little from heartwood and *vice-versa*. By way of contrast, species in sclerophyll forests were highly efficient at nutrient redistribution from both leaves and wood.

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INTRODUCTION

Nutrient cycling within forests is critical for long term maintenance of productivity and stability. It involves nutrient uptake, utilization and accumulation by vegetation, together with the return of nutrients to the soil through litterfall, leaching and root sloughing. Comparisons of nutrient cycles involve considerations of how species are able to obtain nutrients from soils with low nutrient status and then retain the nutrients within systems (Turner, 1975). In order to assess turnover of nutrients, various indices have been developed. For example, turnover of litter on forest floor has been compared by using a 'k' factor which relates the input of litter (L) to the mass of litter (F) on the forest floor. The 'k' factor = L/F and assumes a steady state forest floor weight (Jenny *et al.*, 1949; Olson, 1963; Richards and Charley, 1977) and gives an indication of the rate of loss (decomposition) by the litterfall in relation to accumulation on the forest floor.

Relative efficiency of nutrient acquisition from soil, nutrient utilization requirements and efficiency of redistribution of nutrients can be assessed within the tree component of an ecosystem. These comparisons are difficult, but some can be made. For example, an index of nutrient utilization within a tree is often obtained using foliage nutrient concentrations (Lambert and Turner, 1983; Lambert *et al.*, 1983). Nutrient redistribution may be estimated as withdrawal of nutrients, both during leaf abscission (Ashton, 1976; Attiwill, 1980; Turner and Lambert, 1983) and in heartwood formation (Lambert, 1981). Such estimates have been made in only a few forests in Australia and have been carried out predominantly in stands dominated by a single species (Hingston *et al.*, 1979; Attiwill, 1980; Turner and Lambert, 1983) where monthly leaf litterfall data were compared with those for live leaf material on the trees. In studies of forest stands including a variety of species, and particularly in conditions where organic matter decomposition and tissue leaching can be quite rapid, the use of monthly litterfall samples becomes inappropriate.

Subtropical rainforests are associated with relatively fertile soils (Baur, 1957; Webb, 1969; Lambert *et al.*, 1983) whereas eucalypt forests are on soils with much lower fertility (Baur, 1957; Webb, 1969; Turner and Kelly, 1981). Subtropical rainforests (Baur, 1965) have high species diversity with often in excess of 30 species ha^{-1} in the overstorey. They are notable in northern N.S.W. for the absence of *Eucalyptus* species, a genus which

dominates most other coastal and tableland forest types in N.S.W. During a programme of study in a subtropical rainforest located on the New South Wales Border Ranges, leaf material was sampled from a range of species in order to obtain indices of nutrient distribution and cycling patterns within this forest. Fresh litter was specifically sampled to provide estimates of nutrient redistribution in various species. These data were combined with differences in heartwood and sapwood nutrient concentrations and compared with similar data from coastal sclerophyll forests.

STUDY SITE

The study site was originally described by Lambert *et al.* (1983) and was located in forests of the Border Ranges (153°E, 28°38'S), west of Murwillumbah. The altitudinal range of the forest is 600-1200m above sea level. Annual rainfall is 3000mm. Plots were selected from within subtropical rainforest growth experiments (Burgess *et al.*, 1975; Horne and Gwalter, 1982). Soils from the region are derived from Tertiary volcanic rocks of the Mt Warning Shield and are predominantly of basaltic composition (Stevens, 1976). The basalts have given rise to kraznozems, that is, deep well-structured red clay loams with clay sub-soils having a relatively uniform appearance and depth (Beckman and Thompson, 1976). The soils are high in nutrients, particularly when compared with soils supporting sclerophyllous species (Lambert *et al.*, 1983).

METHODS

Trees were sampled for foliage and wood during logging operations near the study site. Within a species, nutrient variability in foliage concentration was found to be low (Lambert *et al.*, 1983; Lambert and Turner, 1986). Foliage samples were bulked from within the crown but only fully-formed leaves were used; that is, very young or damaged leaves were omitted. Samples were placed in paper bags, oven dried at 70°C, ground and analysed for various chemical elements (Lambert, 1983). The results for overstorey and understorey trees have been reported elsewhere. Wood discs were taken from the stem approximately 1m above the ground. These were air dried and then separated into bark, sapwood and, where present, heartwood. The individual components were ground and analysed for the same chemical elements as the foliage samples (Lambert, 1983).

Freshly-fallen leaf samples were sampled beneath the crown of selected species within the research plot and were those recently fallen so that there was minimal effect due to decomposition and leaching. Where leaves were caught on understorey vegetation, they were preferentially selected so that ground contact was minimized. Acquiring sufficient suitable material of many species was difficult and hence single, bulked samples were used rather than replicates. The leaf litterfall samples were dried, ground and analysed in the same way as foliage samples.

A list of the common names, scientific names and authorities of species sampled on the study site is given in the Appendix.

RESULTS

Results of the analyses are presented in detail in Table 1; trends are summarized in Table 2. Changes in concentration of nitrogen and phosphorus between overstorey leaf and litterfall were relatively minor in most cases. There were obvious exceptions, such as *Dendrocnide excelsa*, *Solanum aviculare* and *Solanum mauritianum*, these tending to be very high in nutrients initially. The other exception was *Orites excelsa* which has relatively low requirements for both phosphorus and nitrogen and appears to be also efficient at retranslocation, that is, there is high nutrient removal by retranslocation even in a situ-

TABLE 1

Mean foliage nutrient concentrations (from Lambert et al., 1983), leaf litter concentrations and estimated concentration changes in tree species in a New South Wales subtropical rainforest

Species	Ash (%)	N (%)	P	Ca	Mg	K	Mn (ppm)	Al	Na	Zn	Fe	B	Cl
<i>Heritiera actinophylla</i>	—	leaf 1.85	765	9930	4050	8450	745	165	150	22	75	43	2225
—	litter	2.02	950	10310	4625	12040	435	145	195	15	90	32	2280
—	change	+1.10	+185	+380	+575	+3590	-310	-20	+45	-7	+15	-11	+55
<i>Neolitsea reticulata</i>	—	leaf 1.80	760	5985	1130	8550	1580	230	2345	40	55	17	1230
—	litter	1.52	680	9795	1830	3440	1680	585	2825	50	250	23	1240
—	change	+0.95	-80	+3810	+700	-5110	+100	+355	+480	+10	+195	+6	+10
<i>Calcdutia paniculosa</i>	—	leaf 1.90	920	13080	12595	10200	1485	3635	1680	29	95	23	1870
—	litter	1.48	815	15900	11255	2330	2120	2155	645	30	95	32	365
—	change	-0.03	-105	+2820	-1340	-7870	+635	-1480	-1035	+1	0	+9	-1505
<i>Euodia micrococca</i>	—	leaf 2.15	1180	11110	3130	6580	800	135	1470	53	69	61	6545
—	litter	1.44	995	12035	3010	1280	800	275	1250	60	190	35	5315
—	change	+2.99	-185	+925	-120	-5300	0	+140	-220	+7	+121	-26	-1230
<i>Dendrocnide excelsa</i>	—	leaf 3.34	2120	30290	7790	25290	95	165	445	35	185	30	11925
—	litter	3.23	1630	41140	5340	8490	145	385	245	40	355	29	3385
—	change	-0.11	-490	+10850	-2450	-16800	+50	+220	-200	+5	+170	+9	-8540
<i>Solanum aviculare</i>	—	leaf 5.21	2660	7790	2800	34050	210	340	215	30	315	27	8040
—	litter	2.95	940	21790	2640	27900	150	140	235	25	140	50	5335
—	change	+1.99	-1720	+1400	-160	-6150	-60	-200	+20	-5	-175	+23	-2705
<i>Cryptocarya erythroxylon</i>	—	leaf 2.08	1150	9155	2410	12185	420	620	1080	75	63	23	2360
—	litter	2.10	1270	12190	1885	-6360	455	1400	590	65	165	35	860
—	change	+0.02	+120	+3035	-525	-5825	+35	+780	-490	-10	+102	+12	-1500
<i>Orites excelsa</i>	—	leaf 1.17	540	6225	1560	4300	1140	6790	220	25	70	22	30
—	litter	0.54	220	5073	1720	1630	2590	2105	550	10	100	20	380
—	change	-0.63	-320	-1152	+160	-2670	+1450	-4685	+330	-15	+30	-2	+350
<i>Geissois benthamiana</i>	—	leaf 1.30	595	15010	4715	7860	960	2285	1305	41	53	44	1640
—	litter	1.26	635	14940	4855	4380	1190	2130	1510	50	140	60	1145
—	change	-0.04	+40	-70	+140	-3480	+230	-155	+205	+9	+87	+16	-495

TABLE 1 (concluded)

Species		Ash (%)	N (%)	P	Ca	Mg	K	Mn (ppm)	Al (ppm)	Na	Zn	Fe	B	Cl
<i>Dysoxylum fraserianum</i>	— leaf	6.67	2.17	1230	10550	4395	17200	35	115	805	25	80	31	6510
	— litter	9.16	1.82	905	18530	5110	11700	70	435	1470	25	325	44	6080
	— change	+2.49	-0.35	-325	+7980	+715	-5500	+35	+320	+665	0	+245	+13	-430
<i>Solanum mauritianum</i>	— leaf	6.95	4.54	885	15910	3545	18220	385	270	550	40	200	69	5070
	— litter	8.94	1.36	655	23220	3980	7950	190	510	600	60	560	54	4600
	— change	+1.99	-3.18	-230	+7310	+435	-10270	-195	+240	+50	+20	+360	-15	-470
<i>Heritiera trifoliolata</i>	— leaf	5.20	1.98	1110	8995	2795	12215	275	55	1170	25	55	27	3735
	— litter	4.32	1.95	970	6945	2395	9470	550	165	515	20	120	55	1410
	— change	-0.88	-0.03	-140	-2050	-400	-2745	+275	+110	-655	-5	+65	-15	-2325
<i>Sloanea woollsii</i>	— leaf	4.30	1.10	755	9255	2950	8025	1005	130	360	30	65	42	1590
	— litter	6.66	0.92	475	14900	4765	5140	815	885	810	15	150	47	1935
	— change	+2.36	-0.18	-280	+5645	+1815	-2885	-190	+745	-450	-15	+85	+5	+345

ation of high nutrient availability (Kelly *et al.*, 1983). Calcium typically increased in concentration in the litter of most species, an exception being *Orites excelsa*. The patterns of other elements were much more irregular (Table 2). Potassium and manganese tended to decline and accumulate respectively. *Caldcluvia paniculosa* and *Orites excelsa* accumulated aluminium in the foliage but the concentration of this element was lower in the litter, the *Orites excelsa* to a higher degree possibly showing different patterns of handling an antagonistic element. Of the 48 samples assessed, heartwood was detectable in only 12 and in these instances relatively few had significant retranslocation of nutrients (Lambert *et al.*, 1983).

Within the non-woody understorey species, nutrients were retranslocated between young and old tissues as in the woody species (Table 3). *Cyathea australis*, for example, redistributed 45% of phosphorus in the aging of fronds. *Archontophoenix cunninghamiana* was an efficient retranslocator of phosphorus (65%) and potassium (96%), although there may be a higher proportion leached as it is difficult to estimate when foliage of this species can be classified as litterfall as the older foliage hangs down next to the stem. *Asplenium nidus* retranslocated much smaller quantities during senescence.

DISCUSSION

Estimates of nutrient retranslocation are relative measures and to understand the ecological significance of nutritional patterns, comparisons with other forest types have been used. Within the subtropical rainforest, retranslocation of nutrients within foliage prior to abscission appears to be relatively low for most overstorey species, however, exceptions were: *Dendrocnide excelsa*, this species having fairly high nutrient requirements; *Orites excelsa*, which is an aluminium-accumulating species and appears to have an efficient system of retranslocation; and two solanaceous species (*Solanum aviculare* and *Solanum mauritianum* which invade and grow immediately after soil disturbance and live for only a relatively short time. It appears they have both high nutrient demands and efficient retranslocation. The level of retranslocation may be compared with that in sclerophyllous species and coachwood which generally grow on nutritionally poorer soils than the subtropical rainforest (Table 4). In these species, phosphorus, nitrogen, magnesium and potassium are all retranslocated, while calcium and aluminium are accumulated. The calcium pattern appears typical of mature foliage in many trees. Further, there were consistently high removals of nutrients in these species during heartwood development. The pattern of heartwood development and retranslocation was either absent or very low in the majority of species sampled in this rainforest.

Generally, nutrient redistribution is an important component, along with uptake, in fulfilling forest stand nutrient requirements (Turner and Lambert, 1983). However, if the general principle is that the subtropical rainforest tree species generally redistribute nutrients at a low level, whereas the sclerophyllous and cool temperate rainforest species are more efficient at redistribution, is this a function of generally higher soil nutrient availability? Further, if large fertilizer quantities were applied to eucalypt species or they were located on more fertile soils, would heartwood production be reduced or litter retranslocation lowered? Eucalypts growing naturally across a range of fertilities do not have significantly different foliage nutrient concentrations (Lambert and Turner, 1983) or nutrient redistribution patterns. This suggests that soil nutrients are not controlling the patterns but rather that they are evolutionarily determined. The reverse situation of growing subtropical rainforest trees on poor sites is harder to test, mainly because it appears that soil nutrients are delineators of species (Turner and Kelly, 1981) and hence rainforest species are out-competed on poor sites.

Within the subtropical rainforest there were some species such as *Orites excelsa*

TABLE 2

Changes in nutrient concentrations between foliage and litter for all species in Table 1. It has been assumed that at least a 10% change in concentration is needed to be significant. If the change is less than 10%, a 0 is listed for that element

Species	Nutrient										
	N	P	Ca	Mg	K	Mn	Al	Na	Zn	Fe	B
<i>Heritiera actinophylla</i>	0	+	0	+	+	-	-	+	-	+	-
<i>Neolitsea reticulata</i>	-	-	+	+	-	0	+	+	+	+	+
<i>Caldeuina paniculosa</i>	-	-	+	-	-	+	(-)	-	0	0	+
<i>Euodia micrococca</i>	-	-	0	0	-	0	+	-	+	+	-
<i>Dendrocnide excelsa</i>	0	-	(+)	-	-	+	+	-	+	+	?
<i>Solanum aviculare</i>	-	-	+	0	-	-	-	0	-	-	+
<i>Cryptocarya erythroxylon</i>	0	+	+	+	-	0	+	-	-	+	+
<i>Orites excelsa</i>	-	-	-	-	-	+	(-)	+	-	+	0
<i>Geissois benthamiana</i>	0	0	0	0	-	+	(0)	+	+	+	+
<i>Dysoxylum fraserianum</i>	-	-	+	+	-	+	+	+	0	+	+
<i>Heritiera trifoliolata</i>	0	-	-	-	-	+	+	-	-	+	-
<i>Solanum mauritianum</i>	-	-	+	+	-	-	+	0	+	+	0
<i>Sloanea woollsi</i>	-	-	+	+	-	-	+	-	-	+	+

TABLE 3
Mean foliage and litter nutrient concentrations and the estimated changes in nutrient concentrations in understorey species

Species	Component	Ash (%)	N (%)	P	Ca	Mg	K	Mn	Al (ppm)	Na	Zn	Fe	B	Cl
<i>Cyathea australis</i>	— frond	6.44	1.73	970	2810	3780	13000	65	9755	1680	35	100	12	14320
	— litter	8.27		505	2670	4440	3420	65	8200	4665	55	140		11735
	— change	+1.83		-465	-140	+660	-9580	0	-1555	+2985	+20	+40		-2585
<i>Archontophoenix cunninghamiana</i>	— frond	6.59	1.20	865	3085	1730	18675	260	35	4945	15	60	6	28145
	— litter	3.33		302	5385	1490	825	365	175	255	15	155		90
	— change	-3.26		-563	+2300	-240	-17850	+105	+140	-4690	0	+95		-28055
<i>Nephrolepis</i> sp.	— frond	6.21		1300	7970	5410	14575	185	585	585	35	290	36	9940
	— litter	3.83	0.85	845	9000	4020	970	310	795	165	50	285	34	115
	— change	-2.38		-455	+1030	+1390	-13605	+125	+210	-420	+50	-5	-2	-9825
<i>Asplenium nidus</i> — mid rib	— new	11.63	1.18	1580	5225	2170	50225	555	60	1240	23	75	31	
	— old	5.61	0.70	470	17910	7245	10605	995	160	1015	20	325	63	340
	— change	-6.02	-0.48	-1110	+12685	+5075	-39620	+440	+100	-220	-3	+250	+32	
— blade	— new	12.11	2.14	2820	13480	4930	37065	885	115	1185	43	100	45	
	— old	16.28	1.80	1465	40910	9415	7400	995	625	3080	55	425	95	850
	— change	+4.17	-0.34	-1355	+27430	+4485	-29665	+110	+510	+1895	+12	+325	+50	

TABLE 4

Published information for various Australian forest species on redistribution from foliage during abscission

Forest Type		N (%)	P	Ca	Mg (ppm)	K	Al	Reference
Wet Sclerophyll								
<i>E. grandis</i>	— foliage	1.47	895	4800	2690	6450	80	Turner and Lambert (1983)
	— litter	0.86	340	7065	2160	1955	230	
	— change	-0.61	-555	+2265	-530	-4495	+150	
<i>E. regnans</i> ^a	— foliage	0.79	780	5730		5730		Ashton (1976)
	— litter	0.87	300	5450		1240		
	— change	-0.12	-480	-280		-4490		
<i>E. pilularis</i>	— foliage	1.21	620	3420	3465	3810	120	Turner and Kelly (1981)
	— litter	0.70	300	12610	2390	1140	330	
	— change	-0.51	-320	+9190	-1075	-2670	+210	
<i>Lophostemon confertus</i>	— foliage	1.61	1205	9525	2735	11035	195	Turner and Kelly (1981)
	— litter	0.81	525	12220	2580	1750	820	
	— change	-0.80	-680	+2695	-155	-9285	+625	
Rainforest								
<i>Ceratopetalum apetalum</i>	— foliage	1.10	505	10365	2990	4540	7275	Turner and Kelly (1981)
	— litter	0.71	210	7890	1740	1030	8200	
	— change	-0.39	-295	-2745	-1250	-3510	+925	
<i>Nothofagus cunninghamii</i>	— foliage		1010					Ashton (1976)
	— litter		300					
	— change		-710					
<i>Athosporia moschatum</i>	— foliage		1500					Ashton (1976)
	— litter		890					
	— change		-630					
Dry Sclerophyll								
<i>E. sieberi</i>	— foliage		440					Ashton (1976)
	— litter		110					
	— change		-330					

^a 2nd year leaf and leaf litter analyses for a mature stand.

which gave a similar pattern to the sclerophyllous pattern of redistribution. Whether this is an indication that the species had evolved on poorer soils and now survive within the subtropical rainforest is difficult to ascertain, but it is suggested that the combination of high litter and heartwood redistribution efficiencies, particularly for phosphorus, is indicative of evolution on soils with low nutrient status.

A further question arises as to the relationship between redistribution during leaf abscission and that during heartwood formation for the rainforest species. For most nutrients there was no relationship, but for phosphorus and nitrogen, there was an inverse relationship (Fig. 1). That is, as the proportion of phosphorus redistributed in leaves increased, the proportion redistributed in heartwood formation or its formation at all, decreased. The exception to this was *Orites excelsa* which, as noted above, tends to have unusual patterns of nutrient utilization compared with other species.

The general pattern for phosphorus in rainforest trees, is that as phosphorus becomes more efficient at redistribution in one type of tissue, it becomes less efficient in another. The species which most noticeably form heartwood are not redistributing during leaf senescence. This is the opposite pattern to that found in *Eucalyptus* and other sclerophyllous species (Fig. 1) where there is simultaneous redistribution from leaf litter

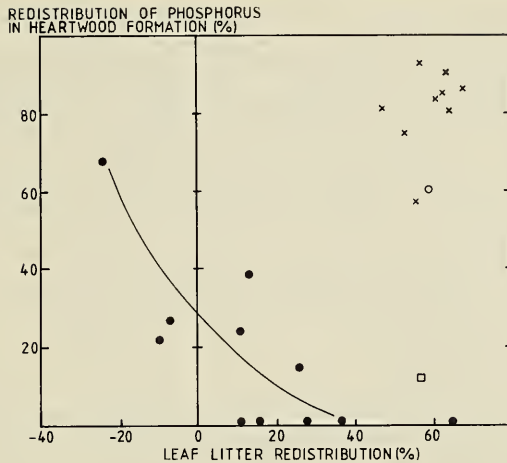


Fig. 1. Relationship between redistribution of phosphorus during heartwood formation and leaf abscission (• — rainforest species; x — eucalyptus and sclerophyllous species; □ — *Ceratopetalum apetalum*; O — *Orites excelsa*).

and heartwood. *Orites excelsa* relates closely to the 'sclerophyllous' pattern which includes *E. pilularis*, *E. dives*, *E. maculosa*, *E. rossii*, *E. rubida*, *E. obliqua*, *E. grandis*, *Lophostemon confertus* and *Casuarina torulosa*, these being the species where mature green leaf, leaf litterfall, sapwood and heartwood concentrations were available. The phosphorus redistribution pattern in coachwood, however, was similar to that found generally in the subtropical rainforest species even though this species grows in differently structured rainforest (Baur, 1965).

Comparisons with other species (Table 4) were based on results for mature leaves on the tree and fresh litter using comparable sampling techniques. Fully-developed younger leaves have nutrient concentrations different to those in older leaves, so that there are different patterns of redistribution taking place within the crown. Further, there are different patterns between different-aged forests of the same species (Ashton, 1975). The pattern for nitrogen was similar to that for phosphorus for the rainforest species. *Orites excelsa* was again found to form a different pattern. Nitrogen was generally not as efficiently redistributed as phosphorus during heartwood formation. *Ceratopetalum apetalum* and *Lophostemon confertus* in this case followed the rainforest pattern, while the eucalypts were differently distributed.

While for most nutrients there are relationships between foliage litter and heartwood redistribution which may be described as specific to species/site, phosphorus and nitrogen have given separate patterns of nutrient cycling. In rainforests, where phosphorus and nitrogen are usually readily available, a certain amount of 'energy' is apparently expended in retaining nutrients in biomass and hence not all tissues are affected. In the case of the lower phosphorus sclerophyllous forest, all available phosphorus is apparently redistributed, this being the primary limiting nutrient. The pattern of *Orites excelsa* possibly indicated that it evolved in a low phosphorus environment.

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APPENDIX

List of common names, scientific names and authorities of species from the study site

Common name	Botanical name
Bangalow palm	<i>Archontophoenix cunninghamiana</i> (H. Wendl.) H. Wendl. et Drude
Birds nest fern	<i>Asplenium nidus</i> L.
Black booyong	<i>Heritiera actinophylla</i> (F. M. Bail.) Kosterm.
Bollygum	<i>Neolitsea reticulata</i> (Meisn.) F. Muell.
Brushbox	<i>Lophostemon confertus</i> (R. Br.) Peter G. Wilson et J. T. Waterhouse
Coachwood	<i>Ceratopetalum apetalum</i> D. Don
Corkwood	<i>Caldcluvia paniculosa</i> (F. Muell.) Hoogl.
Doughwood	<i>Euodia micrococca</i> F. Muell.
Giant stinging tree	<i>Dendrocnide excelsa</i> (Wedd.) Chew
Kangaroo apple	<i>Solanum aviculare</i> Forst. f.
Lace fern	<i>Nephrolepis</i> sp.
Pigeonberry ash	<i>Cryptocarya erythroxylon</i> Maiden et Betche
Prickly ash	<i>Orites excelsa</i> R. Br.
Red carabeen	<i>Geissois benthamiana</i> F. Muell.
Rosewood	<i>Dysoxylum fraserianum</i> (A. Juss.) Benth.
Teak	<i>Flindersia australis</i> R. Br.
Tree fern	<i>Cyathea australis</i> (R. Br.) Domin
White booyong	<i>Heritiera trifoliolata</i> (F. Muell.) Kosterm.
Wild tobacco tree	<i>Solanum mauritianum</i> Scop.
Yellow carabeen	<i>Sloanea woollsii</i> F. Muell.